

CORALLUM INCREASE IN *LITHOSTROTION*

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ABSTRACT. Serial section examination of increase in ten species of *Lithostrotion* from Australia and Great Britain has shown that increase is a valuable specific character, and has confirmed earlier reports that in *Lithostrotion* it is mainly lateral; axial increase has already been reported in *Lithostrotion* from Russia and peripheral increase is herein described in a specimen from Australia.

Four types of lateral increase in *Lithostrotion* are recognized: (1) increase in *L. junceum* (Fleming) in which the daughter corallite has an early aseptate stage after which septa are inserted independently of the septa of the parent; (2) increase in fasciculate species with a narrow dissepimentarium, in which the septa of the daughter are independently inserted; (3) increase in fasciculate species with a wide dissepimentarium, in which the initial septa of the daughter corallite are inherited from the parent; (4) increase in cerioid species, which is related to that in fasciculate species with a wide dissepimentarium.

THE genus *Lithostrotion* Fleming comprises a group of colonial corals possessing a remarkably variable morphology, the variation commonly being expressed as morphologic 'trends' within the genus. Much disagreement exists as to the limits of the generic characters. Although the details of reproduction are quite variable both between and within species and occasionally even within the same corallum, basic patterns of increase do exist within the group, and these can be categorized. *Lithostrotion* lends itself well to ontogenetic studies since adult corallites of most species have an obvious bilateral symmetry, marked by prominently developed axial septa. Septal insertion during the development of new corallites can thus be readily traced.

Reproduction in ten species and one subspecies of *Lithostrotion* was examined in detail by the use of closely spaced acetate peel sections. Six of the species are fasciculate—*L. junceum* (Fleming), *L. arundineum* Etheridge, *L. arundineum* subsp. n., *L. cf. pauciradiale* (McCoy), *L. stanvellsense* Etheridge, *L. sp. nov. 1*, and *L. sp.*; one is semi-fasciculate—*L. cf. martini* Edwards and Haime; and three are cerioid—*L. cf. portlocki* (Bronn), *L. minus* (McCoy), and *L. columnare* Etheridge. These species, which collectively represent most of the basic morphologic types of *Lithostrotion*, were deliberately chosen for study with a view to establishing the general pattern of reproductive variability within the group. An appreciation of the minor factors involved in variation was gained by the examination of two or more examples of increase in all species except *L. cf. pauciradiale*.

Examination was made of only hystero-corallite development. Studies of protocorallite ontogeny have not been made since the preservation of a colony with its protocorallite still intact is extremely rare.

References to increase in *Lithostrotion* have been made by many writers, but details were not discussed until recently when Dobrolyubova (1958) commented on increase in some species from the Russian Platform. Her observations, which are based on thin-section examination, are generally borne out by the present study, but differences of interpretation do exist, these being commented on below.

Matthai (1926) concluded from his study of reproduction in living members of the scleractinian family 'Astraeidae' (Faviida) that an imperfect and often misleading under-

standing of coral reproduction is derived from the study of corallite development alone. As this would probably apply equally well to the Rugosa, the following descriptions deal only with the mechanics of corallite development. Remarks on polyp formation, apart from a few conclusions, are left until additional knowledge is gained on colony formation in the Rugosa.

All the specimens prepared for this study are stored in the Department of Geology and Mineralogy, University of Queensland.

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TERMINOLOGY

Most of the definitions outlined by Hill (1935, 1956) are adopted herein. The following discussion, as well as elaborating on some of the terms pertinent to reproduction in the Rugosa, includes a brief résumé of the results of the present study.

TYPES OF INCREASE

Three main types of increase, namely axial, peripheral, and lateral increase, occur in the Rugosa. A few other types are known, but as these do not occur in *Lithostrotion*, they are not discussed below.

Axial increase, a parricidal condition which involves the splitting of the parent corallite through the axis into two to four daughter corallites, is the least common of the three main types of increase in the Rugosa. Dobrolyubova (1958) reported three species of *Lithostrotion* from the Lower Carboniferous of the Russian Platform which increase by both axial and lateral means. This is the only report of axial increase in the genus.

Peripheral increase, which is usually, but not invariably, parricidal in nature and involves the incorporation of part of the parent corallite into the morphology of the daughter corallite, is known to occur in many fasciculate genera and sporadically in predominantly solitary forms, such as the Devonian *Heliophyllum* Hall and the Viséan *Synplectophyllum* Hill. Peripheral increase is known in only a single specimen of *Lithostrotion*, this being described below. De Groot (1963) referred to peripheral increase in some Spanish Lower Carboniferous lithostrotionids and lonsdaleiids but she apparently used the term for lateral increase in cerioid coralla as described in the present study.

Lateral increase, the commonest type of increase in the Rugosa, is non-parricidal and involves the formation of one or occasionally two or more daughter corallites in the peripheral parts of the calice. Four types of lateral increase are recognized below. The first three listed pertain to fasciculate species, and the last characterizes cerioid species.

(i) Lateral increase in *L. junceum* (Fleming) auctt. is characterized by the daughter corallite forming almost entirely external to the normal edge of the parent calice and having an early aseptate stage (text-fig. 1: 1a-m). The Viséan *Diphyphyllum simplex* (Thomson), a diphyrmorph of *L. junceum*, increases by this means (Dobrolyubova, 1958,

pls. 29–30), and some individuals of *Sudetia lateseptata* Rózkowska (1960, pp. 35–43) of Upper Frasnian age from Poland, have a somewhat similar type of increase.

(ii) Lateral increase in species having a narrow dissepimentarium, is characteristic of those species of *Lithostrotion* with one or two rows of dissepiments (text-fig. 2: 2a–m). The new corallite arises almost at the periphery of the calice, and typically does not inherit septa from the parent. Rózkowska (1960) described a somewhat similar type of increase in *Disphyllum geinitzi* Lang and Smith from the Polish Upper Givetian.

(iii) Lateral increase in species having a wide dissepimentarium, is found in those species of *Lithostrotion* with three or more rows of dissepiments (text-fig. 5: 1a–m). In this type, the parent corallite may or may not insert new septa preliminary to the appearance of the daughter corallite, and the daughter corallite inherits its initial septa from the ends of parent septa, and may develop from well within the parent calice. Both the Ludlovian *Weissermelia lindströmi* (Smith and Tremberth) from Gotland and the Lower Carboniferous D₂ *Corwenia rugosa* (McCoy) from Wales possess lateral increase which may be of this type.

(iv) Lateral increase in cerioid coralla, earlier called intermural increase by Hill (1935, p. 491), is often similar to lateral increase in fasciculate species with a wide dissepimentarium except that the daughter corallite does not grow laterally free of the parent, and the wall dividing the daughter from the parent is of a different nature (text-fig. 6: 1a–m). It is the only type of increase known in cerioid species of *Lithostrotion*.

It is suggested that the term 'intermural' be restricted to increase in which the daughter appears to develop between corallite walls without any particular parent corallite. Dobrolyubova (1958) reported this type of increase in *Lonsdaleia rossica rossica* Stucken-berg of Upper Viséan to Lower Namurian range on the Russian Platform, and I have observed it in a partially diphymorphic corallum of *L. floriformis floriformis* (Martin) from Upper Viséan D₂ beds at the Wrekin, Shropshire, England.

DEVELOPMENTAL STAGES

In the present study, the septa in hysterocorallites which are equivalent to the proto-septa of protocorallites are referred to as *primary septa*. Only four septa are regarded as primary septa in *Lithostrotion*, these being the counter and cardinal septa (axial septa) and the alar septa. Counter-lateral septa are treated as *metasepta* (septa formed after the primary septa) since they are neither distinct in character, nor do they particularly precede metaseptal development.

The hystero-ontogenetic terms of Smith and Ryder (1926), modified by Smith (1945), are applied with some modification in the present study. In *L. junceum* and fasciculate species of *Lithostrotion* having a narrow dissepimentarium, the hystero-brephic stage is characterized by independently inserted primary septa, and is followed by or overlaps the neanic stage, in which metasepta commence to appear, often before all four primary septa are inserted. In cerioid species and in fasciculate species having a wide dissepimentarium, at least in the examples studied, the hystero-brephic stage occurs when the daughter is intimately associated with the parent, and since this condition persists for some time after the appearance of the metasepta, the following stage is referred to as hystero-neanic.

The *late neanic stage* commences when the daughter achieves a bilateral symmetry and assumes a form typical of the ephebic stage except for a smaller corallite size and

fewer septa and dissepiments. The rate of corallite development decreases at this time. In lateral increase in fasciculate species, the late neanic stage is generally initiated before the daughter becomes discontinuous from the parent corallite.

WALL

In lateral increase, contiguous daughter and parent corallites share a common outer wall, and are separated from each other by a wall which is formed in various ways. In cerioid species, this separating wall is identical with the normal wall separating adult corallites. It is secreted by both polyps and often consists of three obvious layers, a median thin, dark layer bounded on either side by fibrous layers, the nature of these fibres being similar to that of the septal fibres.

In fasciculate species of *Lithostrotion*, the wall separating daughter from parent, henceforth referred to as the *partition*, differs from the equivalent wall in cerioid species. It is formed in the region of increase by the dilatation of the ends of both parent and daughter septa forming a thick, generally solid, fibrous wall in which the median dark layer is absent. The partition is confined to the region of attachment of the daughter to the parent. When the daughter becomes discontinuous from the parent, a normal outer wall is developed entirely around each corallite.

Partitions do not invariably separate daughter from parent corallites in fasciculate species. *Lithostrotion* cf. *martini* from the Lower Carboniferous of the British Isles forms a wall analogous to that which divides daughter from parent in cerioid species. Rózkowska (1960, text-figs. 5-7) figured a similar three-layered dividing wall in *Disphyllum geinitzi* Lang and Smith from the Upper Givetian of Poland, but she has subsequently stated (*in litteris*) that the wall is actually two-layered, with the thin dark inner zone being a bituminous residuum rather than a distinct wall layer.

DESCRIPTIONS OF INCREASE IN *LITHOSTROTION*

LATERAL INCREASE

Daughter corallites generally appear one at a time at the periphery of the parent and in no preferred position relative to the axial plane of the parent. Occasionally two or rarely three corallites may appear on the parent, either simultaneously or shortly after one another. Pairs of new corallites typically lie adjacent to each other (text-fig. 2: 2a-m).

Lateral increase always occurs peripheral to the tabularium in the parent corallite. Since the partition (or wall) dividing the daughter from the parent may be formed as far into the calice as the axial edge of the dissepimentarium, daughter corallites arising from parents with a wide dissepimentarium may be positioned well within the parent calice. In fasciculate species, they later grow laterally discontinuous from the parent. In species with a narrow dissepimentarium, the partition forms near the edge of the parent calice, so that in most of its development the daughter corallite overhangs the edge of the calice. In some cases, before the appearance of the daughter corallite, the dissepiments of the parent are locally enlarged, so that the partition, when it forms, is positioned further within the calice than the normal edge of the dissepimentarium of the parent. The effect is thus that the daughter corallite appears to lie partly within the tabularium. This effect

may account for Dobrolyubova's opinion (1958, p. 152) that increase in *L. rossicum* (Stuckenberg) was 'sometimes only in the zone of the dissepimentarium'.

Septal insertion is in the four positions typical of the Rugosa (text-fig. 3). In the early stages, insertion in the cardinal quadrants is accelerated. Septal insertion is commonly somewhat irregular, especially during hystero-brephic and early neanic development. The axial plane of the daughter corallite is radially disposed with respect to the axis of the parent, with the counter septum attached to the partition or, less commonly, to the wall immediately adjacent to the partition, and the cardinal septum attached to the wall opposite the partition. Dissepiments of the parent are not carried forward into the daughter corallite.

I have examined lateral increase in a number of species of *Aphyophyllum* Smith, from Viséan beds in Queensland and New South Wales, and find that the above remarks also apply to this genus.

Type (i): *Lateral increase in L. junceum* (Fleming) auctt.

Text-fig. 1: 1a-m, 2-5; text-fig. 4: 2

Three specimens from Great Britain were examined for increase. Their age and localities are: (a) Upper D₁ or D₂ zone, west of Black Rigg Quarry, near Settle, Yorkshire; (b) D₂-D₃ zones, near Ticknall, Derbyshire; (c) d^{L4} zone (MacGregor, 1960 = Coral Zone 3), near Barness, Edinburgh. Dobrolyubova (1958), pp. 145, 183-6) reported a similar type of increase in *L. junceum junceum* (Fleming) and *Diphyphyllum simplex* (Thomson) from the Lower Carboniferous of the Russian Platform. The latter species is a diphymorph of *L. junceum*.

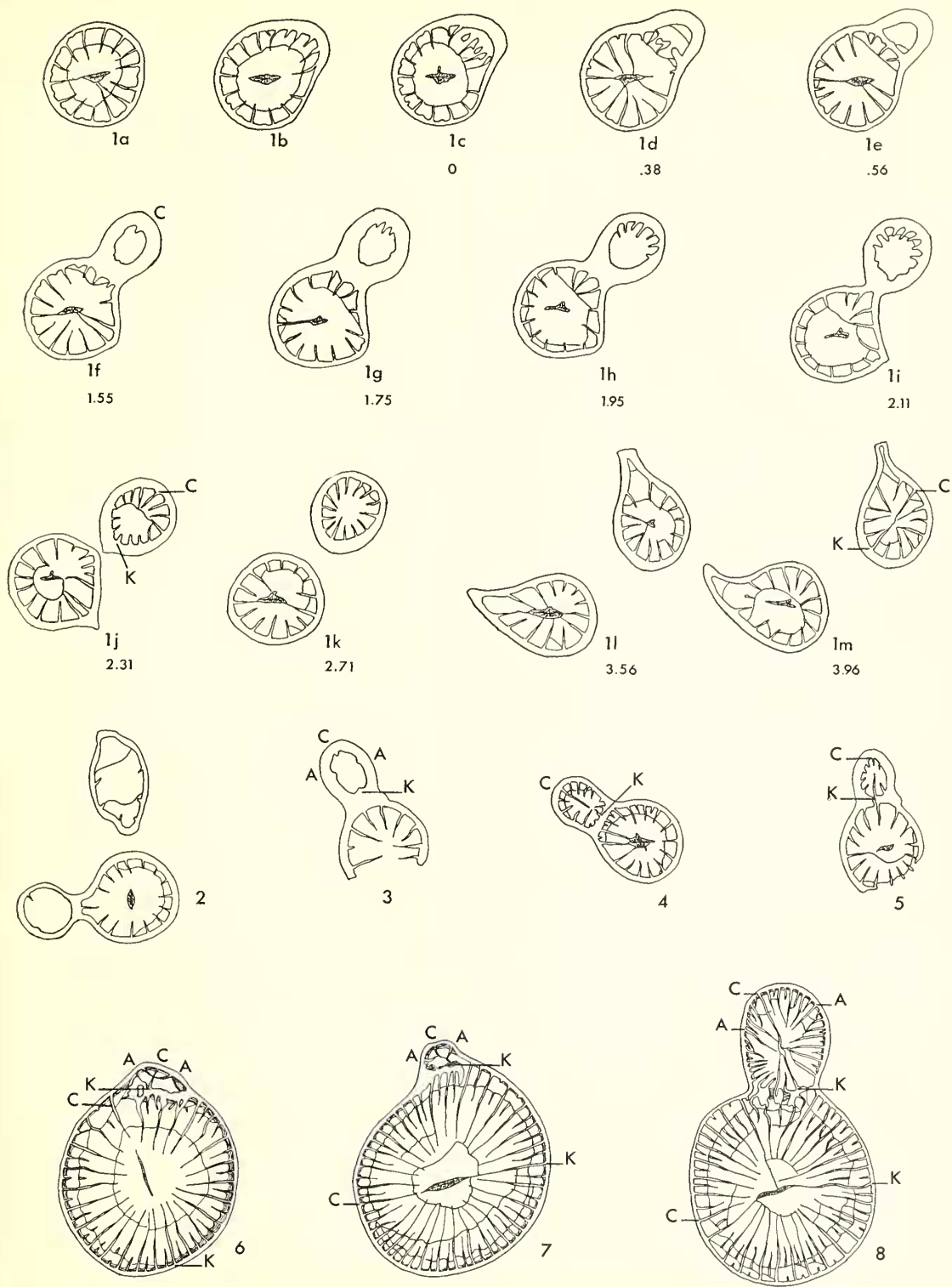
Lithostrotion junceum is one of the most distinctive species of the genus. Besides lacking dissepiments and possessing distinctive types of increase (both this type and axial increase which is later discussed), it often lacks minor septa, corallite diameter is very small, and corallites often throw out tubules connective to their neighbours. The specimen from North Wales figured by Easton (1957, pl. 71, figs. 5, 6) as *L. junceum*, is probably *L. panciradiale*.

Hystero-brephic stage (text-fig. 1: 1c-f, 3). The daughter corallite is developed almost entirely external to the normal circumference of the parent calice, this being achieved by a local outswelling of the wall of the parent. The partition is very thick and is formed by dilatation of the peripheral ends of four, or more typically five major and minor septa at the position originally occupied by the wall of the parent corallite. Although minor septa are absent in many adult corallites, they are apparently invariably

TEXT-FIG. 1. Figs. 1a-5, $\times 8$ approx.; 6-8, $\times 4$ approx. Numbers below figs. 1c-m are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum; A = alar septum.

Figs. 1a-m, 2-5. Lateral increase in *L. junceum* (Fleming). 1a-m, Hystero-ontogenetic sequence, figs. 1a-b are hypothetical drawings based upon other examples of increase in the specimen, F2636, Upper D₁ or D₂ zone, west of Black Rigg Quarry, near Settle, Yorkshire. 2, 3, Nearly aseptate daughter corallites and primary septal swellings, F2636/2, 10, same corallum as above. 4, Elongated cardinal septum, F30206/12, d^{L4} zone (= Coral Zone 3), Barness, near Edinburgh, Scotland. 5, Elongated counter septum, F29972/10, D₂-D₃ zone, Ticknall, Derbyshire.

Figs. 6-8. Lateral increase in *L. arundineum* subsp. n. 6, Primary septa, F28888a/15, Viséan, Baywulla Formation, Yarrol Basin, near Monto, Queensland. 7, Primary septa, F30431a/3, same locality. 8, Fossulae in the later part of the early neanic stage, F30431a/17, same locality.



TEXT-FIG. 1.

present in the zone of increase at the time of formation of the partition. Commonly these minor septa are suppressed after the partition is formed.

Shortly after the partition is formed, small swellings commonly appear on the wall of the daughter corallite in the positions of the axial septa and, less commonly, alar septa (text-fig. 1: 3), but the daughter may then grow distally as much as 1 mm. before typical septa are developed. The order of insertion is variable, but most often the cardinal septum is the first to appear. The counter septum is commonly developed after metasepta are inserted in the cardinal quadrants. Alar septa may or may not precede the metasepta.

Neanic stage (text-fig. 1: 1g-k, 2, 4, 5). This stage overlaps the hystero-brephic stage if counter or alar septa are slow in developing. Metasepta develop rapidly, appearing to emerge from the wall. Insertion is commonly accelerated in the cardinal quadrants. Axial septa may or may not be lengthened more than the metasepta and when such lengthening occurs, it may be of either the cardinal septum (text-fig. 1: 4) or the counter septum (text-fig. 1: 5), but not of both simultaneously. Dobrolyubova (1958, p. 145, pl. 18, figs. 3b, 3b) reported a similar situation in her specimens. Alar septa may be lengthened to the axial region but metasepta typically are not. Minor septa, apart from occasional small swellings on the wall, are absent in daughter corallites which are contiguous with their parents, whether or not the parent possesses them. Columellae are absent or marked by only a slight dilatation of the axial septa if they are united.

In the Yorkshire specimen, the daughter corallites become discontinuous from the parent some 2 to 2.5 mm. distally from the point where increase commenced. The average diameter of the daughter corallite at its point of discontinuity is 1.4×1.6 mm., as compared with an average adult corallite diameter of 2.2 mm. The number of major septa is fourteen, the same as in most adult corallites, and septal spacing is thus closer in young corallites. In one instance, two young corallites become discontinuous from the same parent before septa had emerged beyond a few short projections (fig. 2).

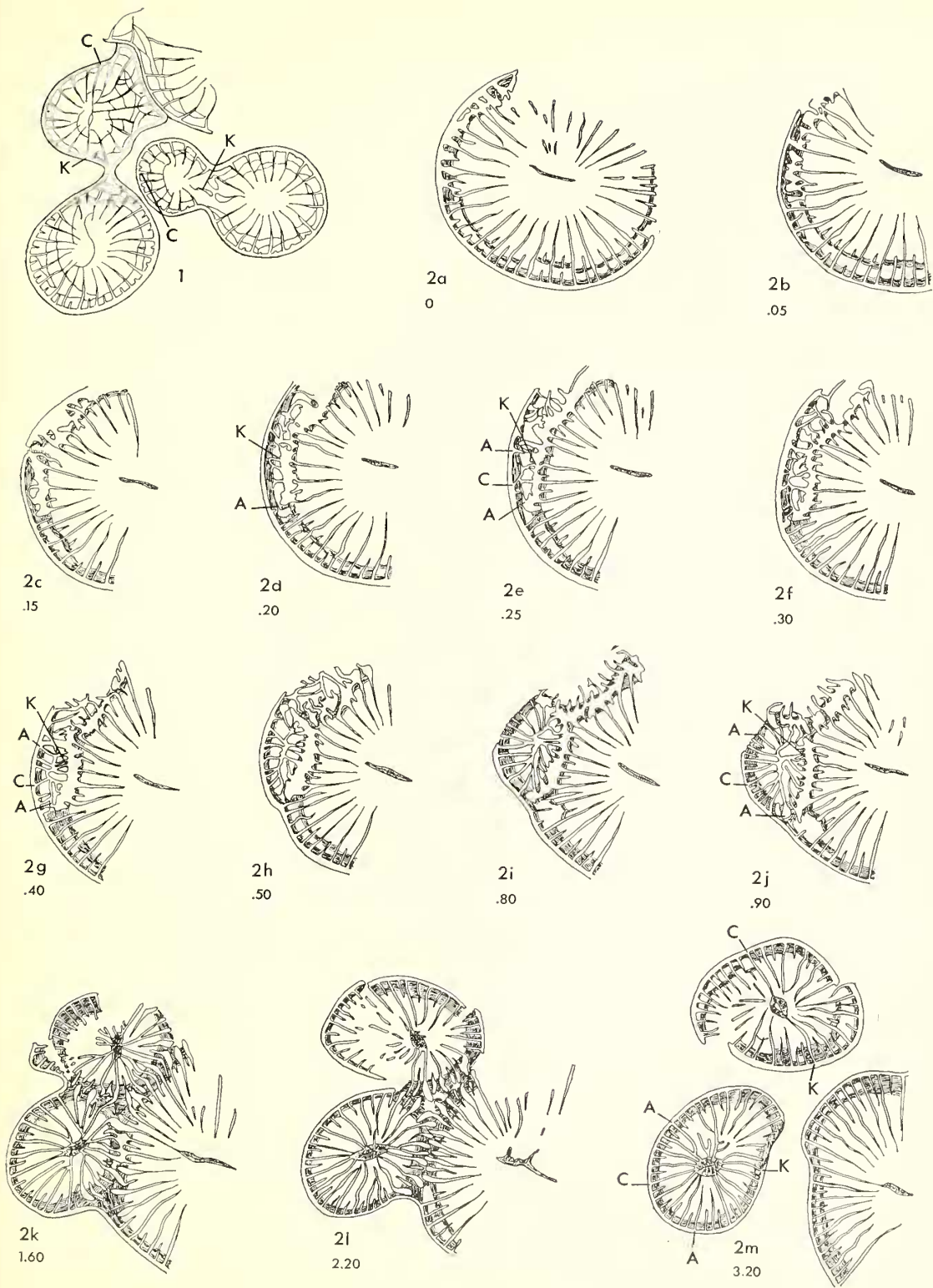
The relation of the diameter and septal number of daughter corallites to those of their adult corallites in the other two specimens is similar to that in the Yorkshire specimen.

After it has become discontinuous, the young corallite gradually grows to the adult stage (text-fig. 1: 1l-m), and a normal columella may develop, depending upon whether or not the corallum has diphymorphic tendencies.

An interesting analogy is found in *Sudetia lateseptata* Rózkowska from the Polish Upper Devonian. Rózkowska (1960, pp. 36-40) found that new corallites in this species are mainly aseptate during the early part of increase, and also that adult corallites throw out connective processes similar to those in *L. junceum*. Rózkowska referred to this type of increase in *Sudetia* as 'syringoporoid', and considered that similar increase occurs in *Peneckiella jevlanensis* Bulvanker and *Donia russiensis* Soshkina, both Upper Frasnian corals from the Russian Platform. Similarities between *L. junceum* and *Sudetia* may

TEXT-FIG. 2. All figures $\times 4$ approx. Numbers below figs. 2a-m are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum; A = alar septum.

Figs. 1, 2a-m. Lateral increase in species with a narrow dissepimentarium. 1, Diphymorphic corallites of *L. arundineum* Etheridge, F44268/20, Viséan, Baywulla Formation, Yarrol Basin, near Monto, Queensland. 2a-m, Hystero-ontogenetic sequence in *L. arundineum* subsp. n., F28888b, from the same locality.



TEXT-FIG. 2.

point to a relationship between the two. It is quite possible that *L. junceum* has a different ancestor from that of the other lithostrotionids.

Type (ii): *Lateral increase in species with a narrow dissepimentarium*

Text-fig. 1: 6-8; text-fig. 2: 2a-m

This type of increase is typical of those species of *Lithostrotion* examined which possess one or two rows of dissepiments. Specimens examined in detail were of *L. arundineum* Etheridge, and *L. arundineum* subsp. n., both of Viséan age from the Baywulla Formation in the central-western part of the Yarrol Basin, near Monto, Queensland, and *L. cf. pauciradiale* (McCoy) of S₂ age from the Scaleber Quarry, near Settle, Yorkshire. This last-named species is conspecific with '*L. cf. martini*' figured by Hudson (1930, pl. 1, fig. 2) from the same locality, and differs from *L. pauciradiale* (*sensu* Hill, 1940, pp. 169-70, text-fig. C) by having a slightly larger corallite diameter and septal number, longer septa (not a diagnostic feature), and tabulae which are more strongly arched up to the columella.

Preliminary to the appearance of the daughter corallite, the region of increase in the parent corallite is modified in the following ways: septa may become wavy and discontinuous from the wall, some minor septa may be suppressed, often sclerenchyme is deposited, and in some corallites, the dissepimentarium is widened a short distance into the tabularium.

Hystero-brephic stage (text-fig. 1: 6-7; text-fig. 2: 2b-d). The partition is formed in a similar manner to that observed in *L. junceum*, but it differs in being thinner, and in some cases, not solidly formed during the period of contiguous development of the daughter corallite. Sclerenchyme usually lines the outer wall, and to a lesser extent, the partition of the daughter corallite; occasionally it is so abundant during the early stages of increase that it masks the initial insertion of septa.

Septa are inserted almost immediately after the formation of the partition, or even before the septa of the parent are withdrawn from the region of increase. Primary septa commonly appear almost simultaneously (text-fig. 1: 6-7), but often their insertion is irregular and they may appear in almost any order and after the insertion of metasepta (text-fig. 2: 2c-e). In one example of increase in *L. arundineum*, axial septa appear to have formed from the prolonged end of a parent septum. Dobrolyubova (1958, pp. 152-5) concluded from her examination of increase in *L. rossicum* Stuckenberga and *L. volkovae* Dobrolyubova, both of which species have one or two rows of dissepiments, that the daughter inherited septa from the peripheral ends of parent septa. One of her figures (1958, text-fig. 27) seems to indicate this, but possibly the study of increase in these species by use of closely spaced serial sections might show that septa are independently inserted. If her conclusions are correct, however, independent insertion of all daughter septa cannot be taken as a consistent feature of this type of increase.

Neanic stage (text-fig. 1: 8; text-fig. 2: 1e-m). This stage commences with the appearance of metasepta, and continues beyond the point of discontiguity of the daughter from the parent corallite. If one or more of the primary septa are inserted late, the hystero-brephic stage overlaps this stage.

As a result of asymmetrical development of the daughter corallite in the early part of this stage, septal insertion is generally not equal between cardinal quadrants or counter quadrants. Eventually, corresponding quadrants are of equal size and septal number.

Septal insertion differs in cardinal and counter quadrants, particularly during the early neanic stage. This is illustrated in text-fig. 3, a graphic representation of septal insertion in the hystero-ontogenetic sequence figured in text-fig. 2: 2a-m. It is typical of insertion in daughter corallites arising by this type of lateral increase. Since serial sections were taken at regularly spaced intervals, the order of insertion is in doubt for those septa

Fig. No.	Distance (mm.)	Cardinal Quadrants		Counter Quadrants	
		Left	Right	Left	Right
2a	0				
2b	.05				
	.10				
2c	.15				1
2d	.20		2 1		K 2 1
2e	.25	1 C	3 2 1	1 2	2 1 3
2f	.30	<u>1</u> 2 3	<u>3</u> 2 <u>1</u>	<u>1</u> 2 3	2 <u>1</u> 4 3
2g	.40	<u>1</u> <u>2</u> <u>3</u>	<u>3</u> <u>2</u> <u>1</u>	<u>1</u> 2 3	2 <u>1</u> 4 <u>3</u>
2h	.50	<u>1</u> 4 <u>2</u> 5 <u>3</u> 6	4 <u>3</u> <u>2</u> <u>1</u>	<u>1</u> 4 <u>2</u> 3	2 <u>1</u> 4 <u>3</u> 5
	.60	<u>1</u> 4 <u>2</u> 5 <u>3</u> 6	4 <u>3</u> <u>2</u> <u>1</u>	<u>1</u> 4 <u>2</u> 3	2 <u>1</u> 4 <u>3</u> 5
	.70	<u>1</u> 4 <u>2</u> 5 <u>3</u> 6	4 <u>3</u> <u>2</u> <u>1</u>	7 6 5 1 4 2 3	2 <u>1</u> 4 <u>3</u> 5 6
2i	.80	<u>1</u> 4 <u>2</u> 5 <u>3</u> 6	4 <u>3</u> <u>2</u> <u>1</u>	<u>7</u> 6 <u>5</u> 8 <u>1</u> 4 2 3	2 <u>1</u> 4 <u>3</u> 5 6
2j	.90	<u>1</u> 4 <u>2</u> 5 <u>3</u> 7 6 8	8 <u>4</u> 7 <u>3</u> 6 <u>2</u> 5 <u>1</u>	<u>7</u> 6 <u>5</u> 8 <u>1</u> 4 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 6
	1.00	<u>1</u> 4 <u>2</u> 5 <u>3</u> 7 6 8	8 <u>4</u> 7 <u>3</u> 6 <u>2</u> 5 <u>1</u>	9 <u>7</u> 6 <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 6
	1.10			9 <u>7</u> 6 <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u>
	1.20			9 <u>7</u> <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u>
	1.30			10 <u>9</u> <u>7</u> <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 9
	1.40			10 <u>9</u> <u>7</u> <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 9
	1.50				
	1.60				
	1.70			10 <u>9</u> <u>7</u> <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 9
	1.80			10 <u>9</u> 11 <u>7</u> <u>5</u> 8 <u>1</u> 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 10 <u>9</u>
	1.90			10 <u>9</u> 11 <u>7</u> 6 <u>5</u> 8 <u>1</u> 4 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 10 <u>9</u>
	2.00			10 <u>9</u> 11 <u>7</u> 6 <u>5</u> 8 <u>1</u> 4 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 10 <u>9</u> 11
	2.10			10 <u>9</u> 11 <u>7</u> 6 <u>5</u> 8 <u>1</u> 4 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 10 <u>9</u> 11
2l	2.20	<u>1</u> 4 <u>2</u> 5 <u>3</u> 7 6 8	8 <u>4</u> 7 <u>3</u> 6 <u>2</u> 5 <u>1</u>	10 <u>9</u> 11 <u>7</u> 6 <u>5</u> 8 <u>1</u> 4 2 3	2 <u>1</u> 4 <u>3</u> 7 <u>5</u> 8 <u>6</u> 10 <u>9</u> 11
			Point of	discontiguity	

TEXT-FIG. 3. Septal insertion in *L. arundineum* subsp. n., figured in text-fig. 2: 2a-m. Septa are numbered according to their order of insertion. Underlined numbers (e.g. 1) = major septa; numbers not underlined = minor septa or initially short major septa; stroked numbers (e.g. 6) = suppressed septa; C, K = point of insertion of cardinal and counter septa; number 1 septum of cardinal quadrants = alar septa.

which are represented in this text-figure as appearing simultaneously. Thus of the septa numbered 4, 5, and 6 which appear at the 0.50 mm. level in the left cardinal quadrant, septum number 6, the major septum, should theoretically have been the first inserted of the three, but this could not be proven. For consistency, these three septa, as well as other such cases of apparently simultaneous insertion, are numbered progressively towards the fossula.

In the cardinal quadrants of the species examined, septal insertion is at first slightly accelerated, and is of the zaphrentid mode with three or four major septa appearing consecutively before any minor septa are inserted. When minor septa appear in these quadrants, they do so two or three at a time between the major septa and remain short, buried in the sclerenchyme which lines the wall. Septal activity then becomes very slow

and major and minor septa subsequently appear alternatively, as is the case with septal insertion in the counter quadrants.

In the counter quadrants, positioned on the attached side of the daughter corallite, insertion is typically in the cyathaxonid mode, with major septa alternating in order of development with minor septa. A short septum which is inserted in the alar fossula subsequently lengthens into a major septum, and during or following this lengthening, two other short septa are inserted on either side of it. The one on the counter side, outside the fossula, is generally the first to appear, and remains short as a minor septum. The short septum on the cardinal side, lying in the alar fossula, lengthens into another major septum which in turn has septa inserted on either side, with the cycle then repeating. Coope (1956) described a similar order of insertion in the later growth stages of *Clisiophyllum* and *Aulophyllum*.

This scheme of septal insertion, which I have also found to occur in *Aphrophyllum hallense* Smith, a cerioid species in Viséan beds in New South Wales, commonly varies in minor details. A particularly noteworthy variation is the quite common suppression of newly inserted minor septa, or rarely major septa, for varying lengths of time in the counter quadrants.

With continuing development, the septal number in the counter quadrants surpasses that in the cardinal quadrants until in the ephebic stage about two-thirds of the total number of septa are present in the counter quadrants. Cardinal and alar fossulae commonly are marked by one or more short, contratingent septa which are newly inserted (text-fig. 1: 8). As septa lengthen, they cease to be contratingent, but if septal insertion is fairly rapid, newly formed contratingent septa maintain the fossular opening. In the late neanic stage, fossulae are generally not obvious. Cardinal fossulae may later reappear in the ephebic stage, this time marked by a shortened cardinal septum.

In non-diphymorphic coralla, the counter and cardinal septa are united from the time of their development; similarly most of the other major septa are united at the axis soon after they are inserted. Conjoined axial septa may or may not be dilatated to form a columella in the early neanic stage. When a columella is first formed, it is irregular in shape and does not assume the typical lithostrotionid form until just before the corallite becomes discontinuous from the parent, at the start of the late neanic stage.

Dissepimental development could not be established in the cardinal quadrants of the species examined since these plates are masked by sclerenchymal deposits at the wall. Not until the late neanic stage do they become obvious. In the counter quadrants, dissepiments develop later than the minor septa, with one complete row present during the late neanic stage. Dobrolyubova (1958, pp. 153-4) noted that while dissepiments are absent during early hystero-ontogeny in *L. rossicum*, a single row is developed at an early stage in the cardinal quadrants in *L. volkovae*.

At the point of discontinuity in all specimens examined, the daughter corallite possesses the diagnostic characters of the species, except that corallite diameter and septal number are smaller than in the ephebic stage. At this point in four corallites of *L. arundineum* subsp. n., septal numbers range from 20 to 22 of each order, and corallite diameters are approximately 5 mm., as compared with adult septal numbers of 26 to 29, and corallite diameters of 7 to 8 mm. The diameter and septal number of corallites at the point of discontinuity in *L. arundineum* and *L. cf. pauciradiale* are similarly smaller than those of their adult stages.

The amount of distal growth between the commencement of increase and the point of discontinuity varies considerably. A range of 2 to 4 mm. is found in *L. arundineum* subsp. n., 1 to 2.5 mm. in *L. arundineum* (a species with small corallites), and 5.5 mm. in the single example of increase studied in *L. cf. pauciradiale*. Septal spacing is slightly narrower in detaching corallites than in the adult.

Between the point of discontinuity and the achievement of the ephebic stage, the rate of corallite expansion and insertion of septa in the daughter is slow.

An interesting variation in hystero-ontogeny was noted in a diphyomorphic corallum of *L. arundineum* subsp. nov., in which two examples of increase were studied (text-fig. 2: 1). Both daughter corallites arise from consistently diphyomorphic, non-columellate parents, and their septa are not united during early hystero-ontogeny. Throughout development in one daughter, axial and other major septa are never united at the axis and a columella does not develop. However, during the late neanic stage of the other, before it becomes discontinuous from the parent, axial septa are lengthened and become united. After it becomes discontinuous, a small, thin columella appears, in spite of the parent being non-columellate.

Type (iii): *Lateral increase in species with a wide dissepimentarium*

Text-fig. 4: 1c; 5

Increase of this type was studied in three species which typically have three or more rows of dissepiments. These species are: *L. cf. martini* Edwards and Haime from an unspecified locality in the British Isles, *L. stanvellenae* Etheridge from the Viséan Bay-wulla Formation in the west-central part of the Yarrol Basin, near Monto, Queensland, and *L. sp. nov. 1* from the same locality as *L. stanvellenae*. Differences exist in their manner of increase, but in all the daughter corallite inherits its initial septa from its parent.

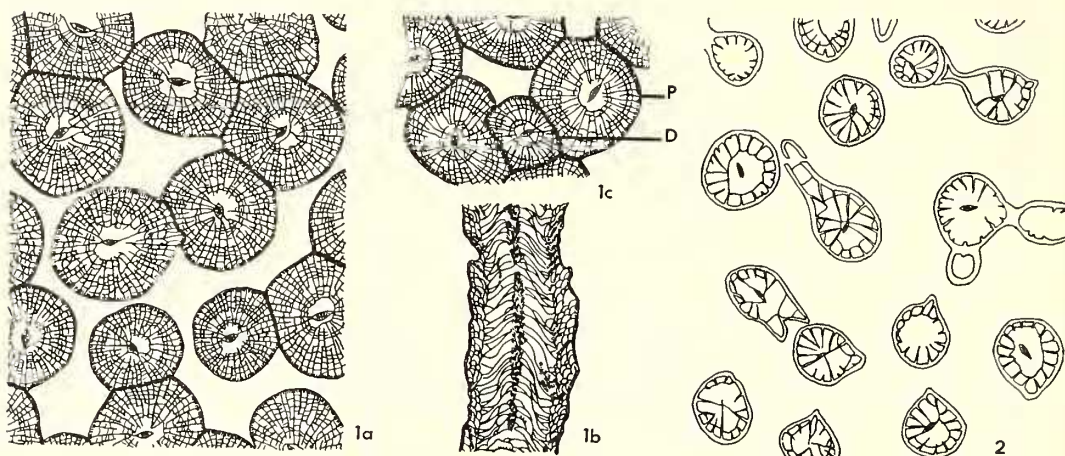
Lithostrotion cf. martini (text-fig. 4: 1a-c; 5), unlike the other two species studied, possesses an unusual morphology which is transitional in nature between the fasciculate and cerioid forms. This is manifested by both the semi-compacted nature of corallites and the characters of increase. Whereas increase is fasciculate in nature by the daughter growing laterally free of the parent, rather than into an elongated corner as occurs in cerioid forms, it is cerioid in nature by the daughter being divided from the parent by a wall, rather than a partition. Moreover, the daughter becomes independent of the parent by simply growing to the side of it and forming a straight-sided contact with it, as is typical in cerioid lateral increase. Were this transitional nature known in *L. martini* (*sensu* Edwards and Haime, 1852, pp. 197-8, pl. 40, figs. 2, 2a-g), I would have no hesitation in regarding my specimen as conspecific with it, although it differs in the minor details of having a slightly larger columella and more strongly arched tabulae.

The following description is based mainly on increase in *L. cf. martini*, in which two examples were studied, but it applies in general detail to that found in *L. stanvellenae*. Increase in this latter species is quite irregular and the progressive development of the daughter corallite could not be studied in as much detail as was done in *L. cf. martini*. Early development in *L. sp. nov. 1*, which differs from the other two species, is mentioned later.

Hystero-brephic stage (text-fig. 5: 1b-g, 2b-e). Increase commences with the insertion of a variable number of short septa in the region of increase in the parent corallite

(text-fig. 5: 1b-c, 2b-c). A variable number is formed, with only one appearing in each loculus. The peripheral ends of these newly inserted septa are located first at the outermost row of dissepiments, but are subsequently lengthened both peripherally to meet the wall and axially a variable distance. Concurrent with their insertion and lengthening is a progressive failure of the dissepiments and a shortening of the minor septa in the region of increase.

Three minor septa of the parent are destined to become the cardinal and two alar septa of the daughter corallite. The counter septum is formed later when the wall (or



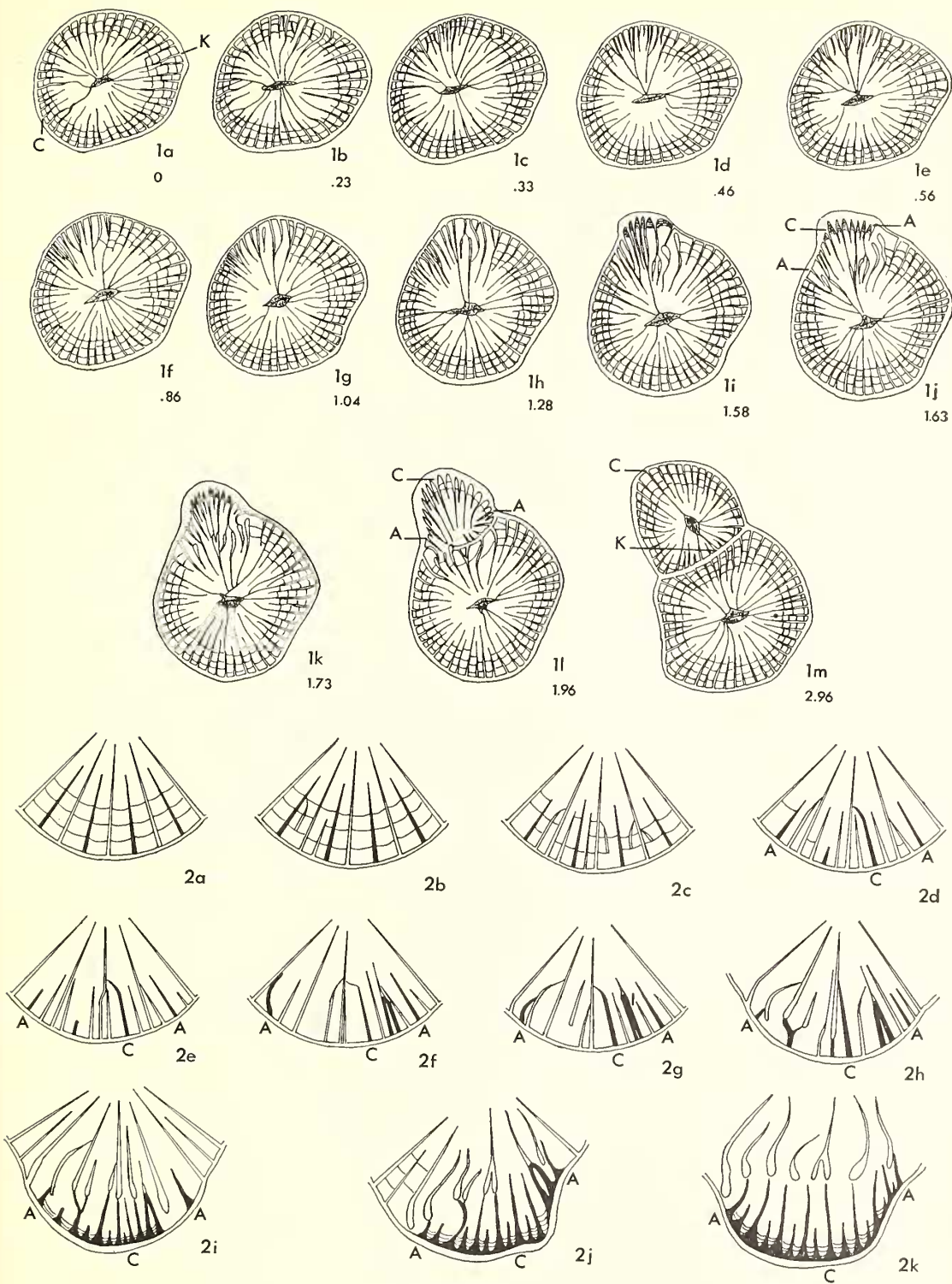
TEXT-FIG. 4. Figs. 1a-c, $\times 2$; 2, $\times 4$. 1a-b, transverse and longitudinal sections of *L. cf. martini* Edwards and Haime, F30508B, C, Lower Carboniferous, unspecified locality, British Isles. 1c, as fig. 1a, showing daughter corallite (D) lying against its parent (P) and encroaching into a neighbouring corallite. 2, *L. junceum* (Fleming), showing connective tubules F2636/18, Upper D₁ or D₂ zone, west of Black Rigg Quarry, near Settle, Yorkshire, England.

partition) is constructed between the daughter and the parent corallite. When four minor septa are involved in the region of increase, one of them is suppressed (text-fig. 5: 1e-f, 2d-f). Some of the newly inserted septa, which number more than four, take the place of these minor septa, and the rest are suppressed, either in the late hystero-brephic, or early hystero-neanic stage.

Hystero-neanic stage (text-fig. 5: 1h-m, 2f-k). During the early part of this stage, the daughter corallite is still intimately associated with the parent and sclerenchymal deposits are common, particularly lining the outer wall of the daughter.

This stage commences with the retreat of major and newly inserted parent septa from the wall in the region of increase. United to the peripheral ends of these septa, which are

TEXT-FIG. 5. Figs. 1a-m, $\times 4$ approx.; 2a-k, not to scale. Numbers below figs. 1a-m are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum; A = alar septum. Figs. 1a-m, 2a-k. Lateral increase in *L. cf. martini* Edwards and Haime. 1a-m, Hystero-ontogenetic sequence, F30508b, unspecified locality, British Isles. 2a-k, Semi-diagrammatic sketches of increase in the above sequence. White septa = parent septa; black septa = septa which will be, or are, those of the daughter.



TEXT-FIG. 5.

their thickest parts, are thin septa. These thin septa are the first metasepta of the daughter corallite, and three form in each cardinal quadrant. As the parent septa retreat axially, the daughter septa lengthen, maintaining their attachment to the wall and to the ends of the parent septa. Variations in metaseptal development occur, but these are of minor significance.

As the metasepta of the daughter lengthen, minor septa are rapidly inserted between them (text-fig. 5: 1j, 2i). When the septa of the parent have completed their retreat, the daughter is divided from the parent corallite either by a wall, as in *L. cf. martini* (fig. 11), which progressively forms across the zone of contact in line with the edge of the dissepimentarium, or by a partition, as in *L. stanvellsense*, which forms in a manner as previously described.

The major septa in the cardinal quadrants of the daughter corallite are attached to the dividing wall when it is first formed, but they almost immediately retreat. The first septa formed in the counter quadrants, which are usually majors and include the counter septum, appear on the dividing wall in the positions previously occupied by the ends of the septa of the cardinal quadrants (text-fig. 5: 1f). Minor septa soon appear between them, often in pairs.

The two axial septa are initially separate, but soon unite in the axial region and form an irregularly shaped columella. The columella does not become typically fusiform until the late neanic stage. Other major septa may be united at the axis in the early hysteroneanic stage (not shown in text-fig. 5), but later they usually do not reach the axial region. A single row of dissepiments in the cardinal quadrants is first obvious just before the wall separating the daughter from the parent corallite is formed and a second row is progressively developed before the daughter grows outside of the parent corallite (text-fig. 5: 1m). Dissepiments are formed later in the counter quadrants.

The maximum diameter of the daughter corallite of *L. cf. martini* when it reaches the point of lying outside of the parent corallite is 5 mm., and its septal number is 20 septa of each order, as compared with a typical adult diameter of 7 mm. and septal number of 24. The relative size and septal number of daughter to parent at the point of discontinuity in *L. stanvellsense* is similar to that in *L. cf. martini*. Approximately 3 to 4 mm. of distal growth occurs in *L. cf. martini* between the start of increase and the separation of the daughter from the parent, and 6 to 7 mm. occurs in *L. stanvellsense*.

Newly formed corallites were not traced up to the ephebic stage. However, supporting observations indicate that subsequent development was slow, and in *L. cf. martini* septa are inserted with their peripheral ends resting against the outermost row of dissepiments, as is the case of insertion during the initial stages of increase in this species. Septa appear to be inserted from the wall in *L. stanvellsense*, but this was not definitely established.

A variation in the above pattern of increase was noted in *L. sp. nov. I*. In this species, septa are not inserted in the parent corallite at the start of increase, and the cardinal and alar septa, as well as the first metasepta in the cardinal quadrants of the daughter corallite are formed at the peripheral ends of parent septa.

Type (iv): *Lateral increase in cerioid species*

Text-fig. 6

Sequences of increase were examined in three cerioid species. Two of them, *L. cf. portlocki* (Bronn) from the D₂ zone, near Victoria Bridge, Menai, Anglesey, Wales, and

L. minus (McCoy) from the S₂ zone at Crummackdale, near Austwick, Yorkshire, exhibit typical lateral increase, but the specimen of *L. columnare* Etheridge, which has lonsdaleoid dissepiments and is from the Upper Viséan Lion Creek Limestone in the northern part of the Yarrol Basin, Stanwell, near Rockhampton, Queensland, has a somewhat different type of increase.

The following description is based on the two British specimens, particularly *L. cf. portlocki*, in which five complete sequences of increase were observed. Increase in *L. columnare* is discussed later.

Hystero-brephic stage (text-fig. 6: 1*b-c*). Increase during this stage is similar to that in *L. cf. martini*. The dissepimentarium is suppressed in the critical area, either simply by a progressive decrease in the number of dissepiments, as in *L. minus*, or by firstly a modification of the dissepiments to a herringbone pattern, followed by their failure, as in *L. cf. portlocki* (text-fig. 6: 1*b-e*). New septa in the parent are inserted simultaneously with the suppression of dissepiments. In the five examples of increase observed in *L. cf. portlocki*, from one to five septa are inserted, and their peripheral ends are located axial to the wall. Four septa are inserted in *L. minus*, but the spacing of serial sections did not permit the establishment of their place of insertion with respect to the wall.

Hystero-neanic stage (text-fig. 6: 1*d-m*). The daughter corallite is still intimately associated with the parent during the early part of this stage which commences with the retreat of the parent septa from the wall in the region of increase.

With this retreat, the first septa in the cardinal quadrants of the daughter corallite appear. They may either be formed independently, as occurs in some corallites of *L. cf. portlocki* (text-fig. 6: 1*d-f*), or at the ends of parent septa and apparently derived from them. Minor septa are inserted between these majors before the dividing wall is formed.

Some of the original septa of the parent are suppressed before and during the formation of the dividing wall, and these are replaced by the newly inserted septa. The dividing wall is formed progressively across the zone of contact just peripheral to where the axial edge of the dissepimentarium was located. It cuts off the peripheral ends of the parent septa (text-fig. 6: 1*g-i*) and these ends form the initial septa in the counter quadrants of the daughter corallite. Minor septa in these quadrants may be developed at this time as well as majors. Septa remain short until the wall is entirely constructed, at which time they are lengthened and united at the axis (text-fig. 6: 1*l*).

In *L. minus*, the columella appears as a swelling at the end of the counter septum as soon as this septum is formed, but in *L. cf. portlocki* the columella does not appear until the late neanic stage, after the axial septa are united at the axis. The first dissepiments in the cardinal quadrants are deposited before the wall is completed (text-fig. 6: 1*g-h*), one row developing at a time.

The late neanic stage is reached shortly after the wall dividing the daughter from the parent is completed (text-fig. 6: 1*l*). Septa at this time are arranged symmetrically and united at the axis, and a narrow dissepimentarium and a typical columella are present. This stage of development is approximately equivalent to the point of discontinuity of daughter corallites in fasciculate species. The rate of corallite development up to this point varies considerably between individuals of *L. cf. portlocki*, ranging from 1.2 to 2.9 mm. between the start of increase in the parent to the attainment of the late neanic stage. In *L. minus*, about 3.8 mm. is involved. The ratio of septal number of daughter to

adult corallites at this stage in both species is approximately 4/5, somewhat similar to that found in lateral increase in fasciculate species.

Following the attainment of the late neanic stage, corallite development becomes very slow. Septa are inserted in the typical rugosan manner in fossulae which are not prominently marked.

Two examples of increase were examined in a lonsdaleoid corallum of *L. columnare* (text-fig. 6: 2a-f). Both daughter corallites are formed entirely within lonsdaleoid areas of the parent calices, and in this respect, their early development more closely resembles that which occurs in some species of *Lonsdaleia* (see Smith, 1916; Dobrolyubova, 1958) than in the cerioid species of *Lithostrotion* which are described above.

The corallum in question is only weakly lonsdaleoid, with most corallites either lacking lonsdaleoid dissepiments or having only small developments of them, mainly in their elongated corners. The two corallites which exhibit increase, however, have notably wide lonsdaleoid areas. Whether this is simply a coincidence, or whether it suggests some relationship between increase and lonsdaleoid dissepiments, is not known at present.

The daughter corallite arises at the edge of the parent calice (text-fig. 6: 2a). Although septa of the parent are expressed as short developments on the upper surfaces of the lonsdaleoid dissepiments, none extend continuously across the lonsdaleoid dissepimentarium to the region of increase during early hystero-ontogeny; hence all daughter septa seem independently inserted. Sclerenchymal deposits are initially present in the daughter corallite, but these soon disappear.

During the hystero-brephic and early hystero-neanic stages of development, the daughter corallite is semi-circular in shape and is divided from the parent by a thin wall (text-fig. 6: 2a-e). Corallite expansion occurs entirely within the parent calice. In neither of the two developing corallites examined were the axial septa the first to be inserted, owing to the early asymmetrical development of these corallites. Primary septa and some metasepta are united at the axis soon after they are inserted, and interseptal dissepiments are formed at an early stage of development.

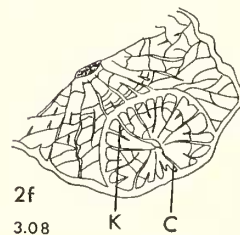
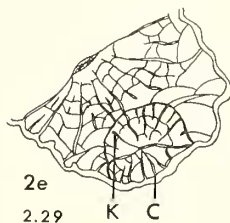
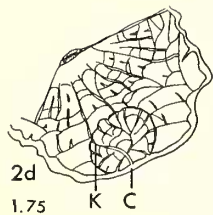
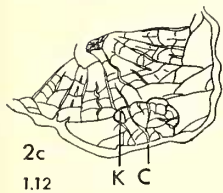
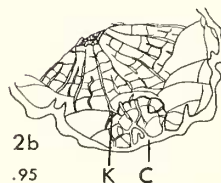
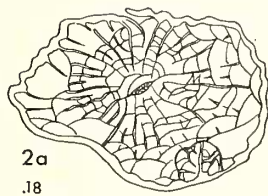
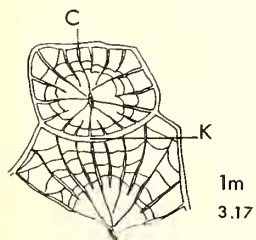
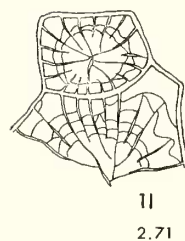
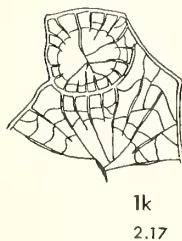
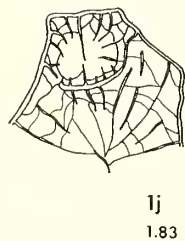
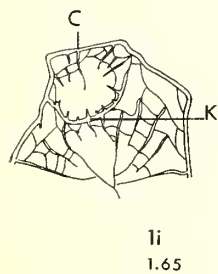
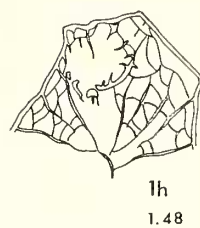
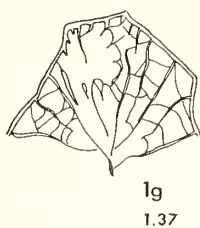
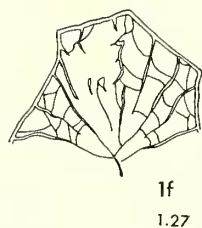
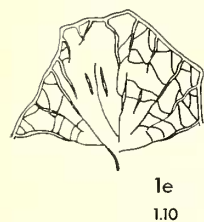
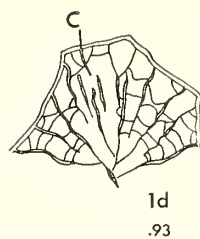
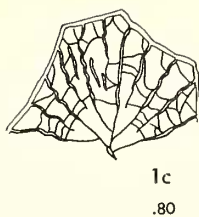
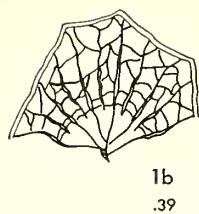
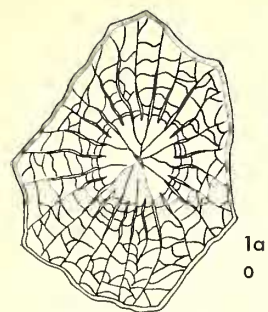
Upon reaching the late neanic stage (text-fig. 6: 2f), the daughter corallite gradually assumes a sub-hexagonal or similar shape. It occupies the entire width of the lonsdaleoid area of the parent, and later growth is only in a distal direction. The wall dividing the daughter from the parent is thickened and becomes a typical intercorallite wall. A single row of interseptal dissepiments is incompletely developed around the corallite, and lonsdaleoid dissepiments are absent, except for a few which occur between some minor septa and the wall.

This type of increase differs considerably from lateral increase in non-lonsdaleoid cerioid coralla. Further studies may recognize it formally as a separate type, perhaps characteristic of lonsdaleoid cerioid species, and epitomized by increase in *Lonsdaleia*.

TEXT-FIG. 6. Figs. 1a-m, $\times 6$ approx.; 2a-f, $\times 4$ approx. Numbers below figs. 1a-m are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum.

Figs. 1a-m. Lateral increase in *L. cf. portlocki* (Bronn), Hystero-ontogenetic sequence, F31047, D₂ zone, near Victoria Bridge, Menai Strait, Anglesey, Wales.

Figs. 2a-f. Lateral increase in *L. columnare* Etheridge, Hystero-ontogenetic sequence, F44601, Upper Viséan, Lion Creek Limestone, Yarrol Basin, Stanwell, near Rockhampton, Queensland.



TEXT-FIG. 6.

PERIPHERAL INCREASE

Text-fig. 7: 1a-b, 2a-m

Peripheral increase is known in only a single specimen of *Lithostrotion*, this being *L. sp.*, a koninckophylloid form from the Upper Viséan Riverleigh Limestone in the southern part of the Yarrol Basin, near Mundubbera, Queensland. Hill (1934, pl. 10, fig. 31) illustrated one of the three examples of peripheral increase present in this specimen. A single example of lateral increase is also present. This was figured by Hill (1934, pl. 10, fig. 31) and is apparently an aberrant type in which the partition dividing daughter from parent is suppressed at an early stage of increase and the two corallites remain contiguous until after the daughter has achieved the ephebic stage of development.

The following description is based on examination of serial sections of one example of peripheral increase, and thin and polished sections of the other two examples.

From four to eight corallites are formed at different levels in the peripheral parts of the parent calice. Generally, the nearer to the calical rim that a corallite is formed, the smaller is its initial size. The newly formed corallites develop at varying rates.

Corallites are not necessarily formed in the peripheral regions of the calice. In the two other examples of peripheral increase, one of which is illustrated herein (text-fig. 7: 1a-b) a corallite appears well within the periphery, and is one of the first to be formed. The development of the corallite in this position was not traced in detail, but it is similar in appearance to the daughter corallites formed at the periphery.

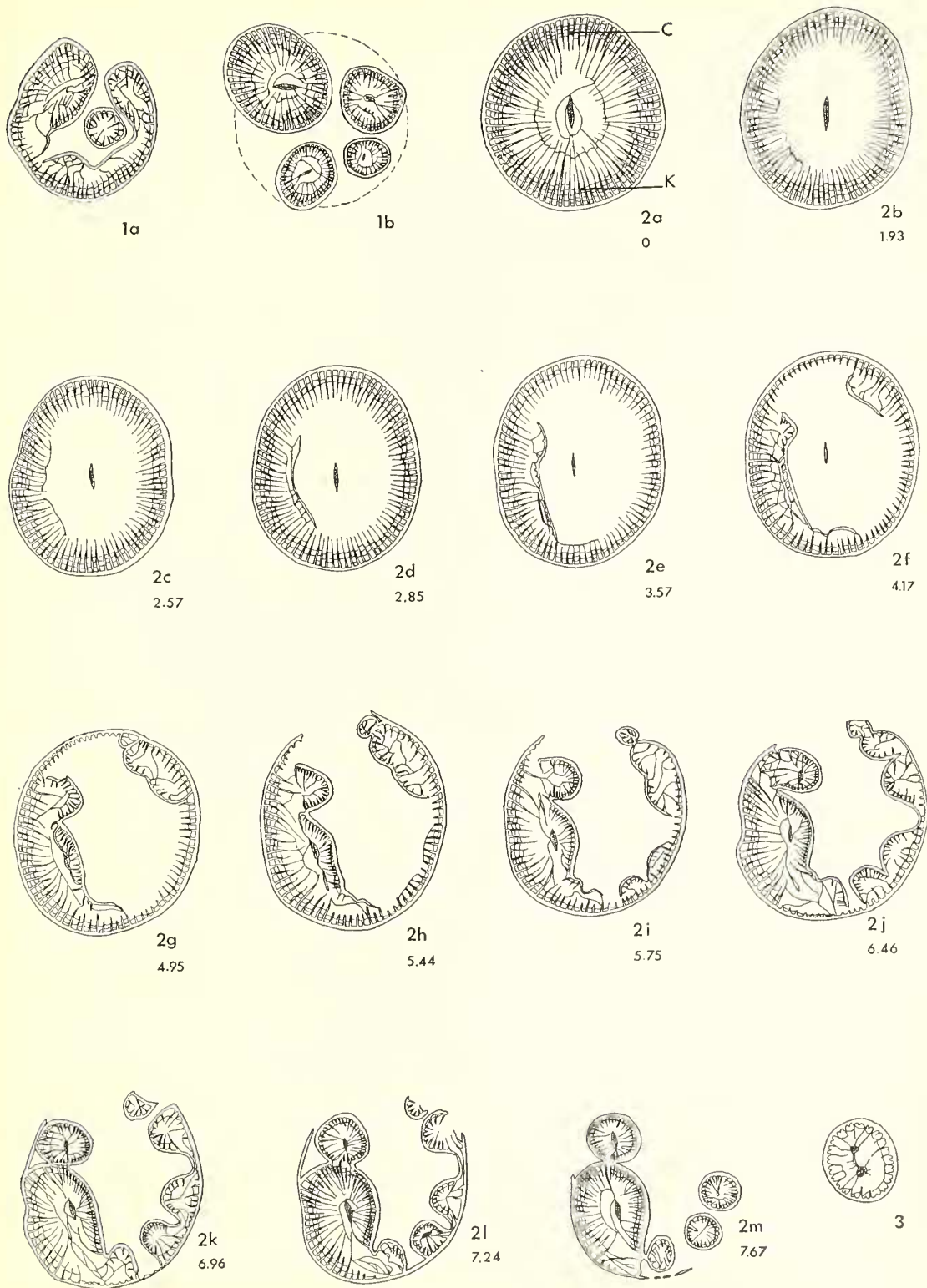
Before increase, septa in the calice are shortened in a normal manner until that point when part of the periphery is modified to accommodate the lowermost of the daughter corallites formed (text-fig. 7: 2b). A number of thin walls are formed at the axial ends of major septa and at varying levels in the calice, ranging from near the base to near the top. These walls are of differing lengths, and are eventually resolved into the inner walls of from one to three corallites. They are sub-symmetrically arranged on either side of the axial plane of the parent but are not as equally ranged around the periphery of the calice as are those in the Wenlockian *Entelophyllum articulatum* (Wahlenberg) or the Carboniferous *D₂ Nemistium edmondsi* Smith (see Smith and Tremberth, 1929; Smith, 1928).

When septa are enclosed by a wall, they either cease to shorten distally, or more commonly, continue to shorten but at a slower rate than the unenclosed septa. Enclosed septa are usually incorporated into the morphology of the daughter corallite, but some continue shortening until they disappear, later to be replaced by newly inserted septa. Almost as soon as the enclosing wall is formed, it commences to migrate towards the axis of the parent and becomes disunited from the major septa which were attached to it

TEXT-FIG. 7. Figs. 1a-b, 2a-m, $\times 2$ approx.; 3, $\times 5$ approx. Numbers below figs. 2a-m are cumulative distances of distal growth in mm. C = cardinal septum; K = counter septum.

Figs. 1a-b, 2a-m. Peripheral increase in *Lithostrotion sp.* 1a-b, Two consecutive stages of development, dashed line indicates the approximate original position of the parent calice, F2965h, j, Upper Viséan, Riverleigh Limestone, Yarrol Basin, near Mundubbera, Queensland. 2a-m, Hystero-ontogenetic sequence of another example from the same specimen as figs. 1a-b.

Fig. 3. Axial increase in *L. junceum junceum* (Fleming), *C₁²⁹¹*, Russian Platform. Drawing is based on Dobrolyubova, 1958, pl. 18, fig. 1b.



TEXT-FIG. 7.

(text-fig. 7: 2d). Short major septa appear on this wall at many points where peripheral septa were attached. Additional major septa soon appear on the dividing wall, followed shortly by minor septa. The septa on the dividing wall lengthen to a varying extent and the wall is modified in such a way that the one or more daughter corallites which it encloses gradually assume a sub-circular shape. A columella is not developed until one or both axial septa are lengthened to the axis. In the largest corallite formed, this occurs almost immediately, but in some of the others, a columella had still not formed by the last observed stage of their development, up to 3 mm. above their initial development. The axial plane of the daughter corallite is not orientated radially with respect to the axis of the parent, as it is in lateral increase, but approximately at right angles to this direction (text-fig. 7: 1b, 2f).

From one to three rows of parent dissepiments are incorporated into the morphology of those daughter corallites which also inherited parent septa. A single row of dissepiments is formed between septa attached to the dividing wall, shortly after these septa are inserted. A second and third row of dissepiments are progressively formed around the corallite as it increases in size and septa become longer.

The late neanic stage of development (fig. 1b) is achieved when corallites grow free of the parent calice. Development thenceforth resembles that in corallites formed by lateral increase.

AXIAL INCREASE

Dobrolyubova (1958) reported axial increase in *L. junceum junceum* (Fleming), *L. caespitosum* (Martin), and *L. scoticum* Hill, and also in three species of *Diphyphyllum*, all of which are from Lower Carboniferous deposits on the Russian Platform. In all but one of the species of *Diphyphyllum*, lateral increase occurs as well. Dobrolyubova (1958) called axial increase 'деление' which I have translated as 'division' (rather than the dictionary alternative, 'fission').

Her description and illustration of axial increase in *L. junceum junceum* (1958, p. 145, pl. 18, fig. 1b; herein refigured in text-fig. 7: 3) show it to be particularly unusual. The parent corallite diameter and septal number are nearly doubled, and twin columellae appear; then follows the development of a wall delimiting two new corallites which occupy the entire calice of the parent.

Another type of increase in *L. junceum junceum*, called 'connective tubular' increase, was named and described by Dobrolyubova (1958, p. 145, pl. 18, fig. 1b). She considered that a young corallite developed in a connective tubule which the parent had thrown out to a neighbour. However, the example which she illustrates appears to be lateral increase in which the contiguous daughter corallite is elongated to form a tubule connective to a neighbouring corallite. This elongation is common in laterally arising immature corallites of *L. junceum* auctt. (see text-fig. 1: 1m, 2; text-fig. 4: 2) and should not be regarded as a particular type of corallum increase.

CONCLUSIONS

1. The mode of increase in *Lithostrotion* is of such variable character that it has limited generic value. This is also known in other rugosan genera and Matthai (1926, p. 351) noted a similar situation in scleractinian corals.

2. The differences in the type of lateral increase between fasciculate and cerioid forms of *Lithostrotion* may justify their generic separation.

3. Hystero-ontogenetic development in *Lithostrotion* seems to confirm the suggestion of Smith and Lang (1930, p. 179) that *Diphyphyllum* arose from *Lithostrotion*, and not the reverse, as was suggested by Minato (1955, text-fig. 20).

4. Axial and peripheral increase are without equivalents in the Scleractinia, but lateral increase in which the daughter corallite inherits septa from the parent resembles the distomodaeal condition of intratentacular budding.

5. Laterally arising hystero-corallites in which the septa are all independently inserted, appear to undergo almost completely independent development, and may mirror the ontogenetic development of their protocorallites.

REFERENCES

- COOPE, G. R. 1956. The insertion of septa in the later growth stages of clisiophyllid corals. *Geol. Mag.* **93**, 233–41, pl. 9.
- DOBROLYUBOVA, T. A. 1958. Lower Carboniferous colonial tetracorals from the Russian platform. *Trav. Inst. paléont. Acad. sci. U.R.S.S.* **70**, 1–224, 38 pl. [in Russian].
- EASTON, W. H. 1957. On the tetracoral *Lithostrotion harmodites* Milne-Edwards and Haime. *J. Paleont.* **31**, 616–22, pl. 71.
- EDWARDS, H. M. and HAIME, J. 1852. A monograph of the British fossil corals. Part 3. Corals from the Permian formation and the Mountain limestone. *Palaeontogr. Soc. [Monogr.]*, 147–210, pl. 31–46.
- GROOT, G. E. DE, 1963. Rugose corals from the Carboniferous of Northern Palencia (Spain). *Leid. geol. Meded.* **29**, 1–123, 26 pl.
- HILL, D. 1934. The Lower Carboniferous corals of Australia. *Proc. roy. Soc. Qd.* **45**, 63–115, pl. 7–11.
- 1935. British terminology for rugose corals. *Geol. Mag.* **72**, 481–519.
- 1938–41. A monograph on the Carboniferous rugose corals of Scotland. *Palaeontogr. Soc. [Monogr.]*, 213 pp., 11 pl.
- 1956. Rugosa; In *Treatise on Invertebrate Paleontology* (R. C. Moore, Ed.). Part F: *Coelenterata*, pp. 233–324. Univ. Kansas Press and Geol. Soc. Amer.
- HUDSON, R. G. S. 1930. The age of the ‘*Lithostrotion arachnoideum*’ fauna of the Craven lowlands. *Proc. Leeds phil. Soc. (Sci. Sect.)*, **2**(2), 95–101, pl. 1.
- MACGREGOR, A. G. 1960. Divisions of the Carboniferous on Geological Survey Scottish maps. *Bull. geol. Surv. G.B.* **16**, 127–30.
- MATTHAI, G. 1926. Colony-formation in astraeid corals. *Phil. Trans. roy. Soc. Lond. (Ser. B)*, **214**, 313–67, pl. 24–28.
- MINATO, M. 1955. Japanese Carboniferous and Permian corals. *J. Fac. Sci. Hokkaido Univ. (Ser. 4)*, **9**, 1–202, 43 pl.
- RÓŹKOWSKA, M. 1960. Blastogeny and individual variations in tetracoral colonies from the Devonian of Poland. *Acta. palaeont. polon.* **5**, 3–64.
- SMITH, S. 1916. The genus *Lonsdaleia* and *Dibunophyllum rugosum* (McCoy). *Quart. J. geol. Soc. Lond.* **71**, (for 1915), 218–72, pl. 17–21.
- 1928. The Carboniferous coral *Nennistium edmondsi*, gen. et sp. n. *Ann. Mag. nat. Hist. (Ser. 10)*, **1**, 112–20, pl. 5.
- 1945. Upper Devonian corals of the Mackenzie river region, Canada. *Spec. Pap. geol. Soc. Amer.* **59**, viii+126 pp., 35 pl.
- and LANG, W. D. 1930. Descriptions of the type-specimens of some Carboniferous corals of the genera ‘*Diphyphyllum*’, ‘*Stylastraea*’, *Aulophyllum*, and *Chaetetes*. *Ann. Mag. nat. Hist. (Ser. 10)*, **5**, 177–94, pl. 7–8.
- and RYDER, T. A. 1926. The genus *Corwenia*, gen. nov. *Ibid. (Ser. 9)*, **17**, 149–59, pl. 5–6.
- and TREMBERTH, R. 1929. On the Silurian corals *Madreporites articulatus* Wahlenberg, and *Madrepore truncata* Linnaeus. *Ibid. (Ser. 10)*, **3**, 361–76, pl. 7–8.

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